

6. *The Lower Jaw Articulatory Region in some Pristerognathid Therocephalians.* By LIEUWE D. BOONSTRA, D.Sc.

(With 4 text-figures)

In the course of the preparation of a paper, mainly of a taxonomic nature, for the *Annals of the South African Museum* on the hundred-odd specimens of Therocephalians from the *Tapinocephalus*-zone preserved in the South African Museum, I have determined certain points in the structure of the posterior part of the lower jaw and the relations of the quadrate, quadratojugal and squamosal.

A short account of the structure in some of the better-preserved specimens is presented here. New genera and species mentioned here will be fully described in the forthcoming taxonomic paper referred to above.

*SCYMNOSAURUS FEROX* (fig. 1)

A specimen collected by me on the farm Rietkuil in the district of Beaufort West (S.A.M. 9084) consists of a fairly good skull and parts of some limb-bones. By direct comparison with the type in our collection I have identified it with *Scymnosaurus ferox*. Natural weathering has partly exposed the mandibular articulatory region, but also unfortunately removed the lateral surface of the quadrate, quadratojugal and the lateral edge of the squamosal.

The dentary has a concave posterior edge overlapping the angular and its dorso-posterior coronoid process does not extend above the subtemporal arch but is directed more posteriorly in the direction of the squamosal.

The angular has a fairly large lateral face with a prominent dorso-ventral ridge and a lesser ridge roughly at right angles. The anterior half of its ventral edge is fairly thick, but the posterior half has a double thin edge—the outer being the reflected flange. Posteriorly the outer (reflected) flange extends to the surangular and ventrally it underlaps the articular. Dorsally there is a small notch, anterior to which the angular apparently overlapped the outer surangular face. This dorsal notch, not exposing the outer surface of the inner angular sheet, but instead the external surangular surface, thus has different relations than in other Pristerognathids where this region has been described. A notch in the ventral edge indicates the level to which the reflected flange usually extends posteriorly in other Pristerognathids.

Externally the surangular shows a thickened rounded and curved dorsal and postero-dorsal girder forming the edge of the mandible. Further ventrally the surangular curves firmly round the lateral surface of the articular and, with the internal prearticular, transmits the stresses arising anteriorly to the articular bone.

The articular is a comparatively small bone of peculiar shape; externally a tongue extending dorsally is anteriorly clasped by the surangular and posteriorly

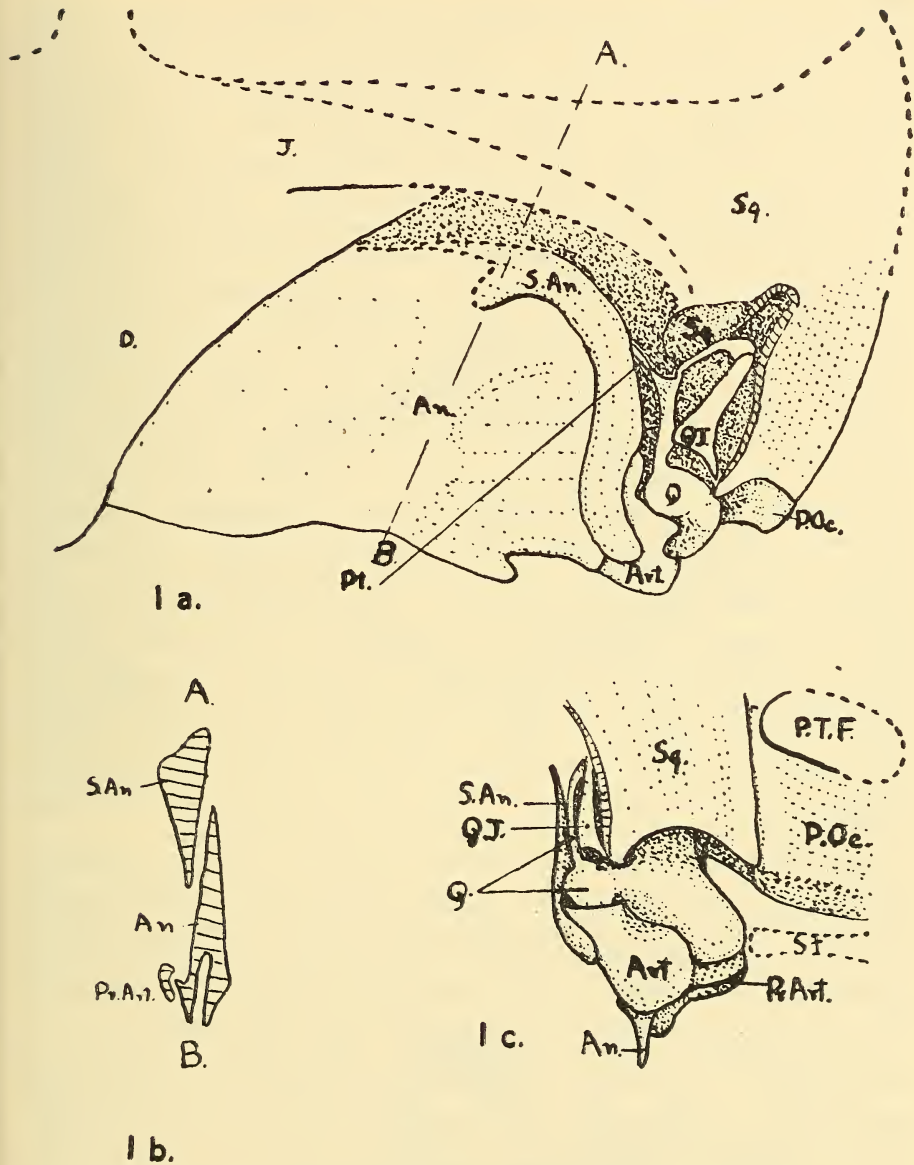


FIG. I.—*Scymnosaurus ferox*. S.A.M. 9084, Rietkuil, Beaufort West. ( $\times \frac{2}{3}$  nat. size.)

- a. Lateral view. The lateral surface of the quadrate, quadratojugal and squamosal has been weathered away so that these elements are seen in section.  
 b. Cross-section of above at A.B.  
 c. Oblique postero-lateral view. The lateral edge of the squamosal, quadrate and quadratojugal weathered and seen in section.

These and subsequent figures are all ortho-projections taken with a pantograph.

An.—angular. Art.—articular. B.Oc.—basioccipital. B.Sph.—basisphenoid. Cor.—coronoid. D.—dentary. Ep.Pt.—epipterygoid. Ex.Oc.—exoccipital. F.J.—foramen jugale. I.P.—interparietal. J.—jugal. Pa.—parietal. P.O.—postorbital. P.O.c.—paroccipital. Pr.Art.—prearticular. Pr.Ot.—prootic. P.T.F.—posttemporal fenestra. Pt.—pterygoid. Q.—quadrate. Q.J.—quadratojugal. S.A.(n)—surangular. S.Oc.—supra-occipital. Sq.—squamosal. St.—stapes. Tab.—tabular.

forms the front face for the articulation with the quadrate condyle; it then extends posteriorly to form the ventral part of the articulatory surface, but no retro-articular process is developed. In posterior view it is seen that the articular has a dorsal spur, which, if it extends anteriorly, must form a ridge dividing the articulatory surface into a smaller lateral concavity and a larger median concavity. The quadratic condyle would thus be bipartite with a smaller rounded outer and an inner larger roller-shaped condyle. Medio-ventrally the under-surface of the articular is clasped by the prearticular, which transmits the greater part of the thrust from the anterior part of the mandible to the articular.

Only part of the quadrate is exposed in lateral and in posterior view. Its lateral surface has been somewhat weathered away so that the drawing (fig. 1a) really shows a section face. The apparent bipartite nature of the quadratic condyle has been noted above. In section the outer condyle has a circular outline. From the antero-dorsal corner of this condyle the lateral edge of the quadrate is seen extending dorsally to meet the squamosal. Further medially a flange of the squamosal clasps the quadrate from above. From the antero-median corner of the quadrate a process stretches antero-medially to meet the quadrate ramus of the pterygoid. In posterior view it is seen that from the external condyle the quadrate extends medially, forming a transverse mass forming the major part of the articulatory surface. Dorsal to this transverse body the quadrate extends dorsally as a strong pillar of which the posterior surface is overlapped by a descending sheet of the squamosal. The medial face of the quadrate abuts against the latero-anterior corner of the strong paroccipital.

On the median surface of the internal condyle there appears to be a shallow depression for the reception of the distal end of the stapes. The tympanic membrane must have been situated in this region, but except for the ventral squamosal edge no other points of attachment can be determined.

The quadratojugal is only seen in section, where it is seen as a triangular element with its base resting on the postero-dorsal surface of the rounded external condyle and its apical part lying posterior to the ascending column of the quadrate and in the hollow between this and the descending flange of the squamosal. The median limits of the quadratojugal and the quadrate foramen are in posterior view hidden by the descending flange of the squamosal.

The squamosal has its lower antero-lateral edge weathered away and a section medial to this is shown in the figure. There is thus exposed much of the quadratojugal, the upper part of the quadrate and the internal forwardly directed domed sheet of the squamosal. All of which would be covered laterally by the squamosal when fully present. In posterior view the descending sheet of the squamosal covers the quadratojugal and most of the quadrate above the condyles. Its ventral edge is concave and probably served as an edge of attachment for the tympanic membrane. The median edge of the descending sheet of the squamosal forms a backwardly directed ridge where it abuts against the paroccipital. This ridge forms the median wall of the auditory groove, which is thus situated directly dorsal of the probable location of the tympanic membrane.

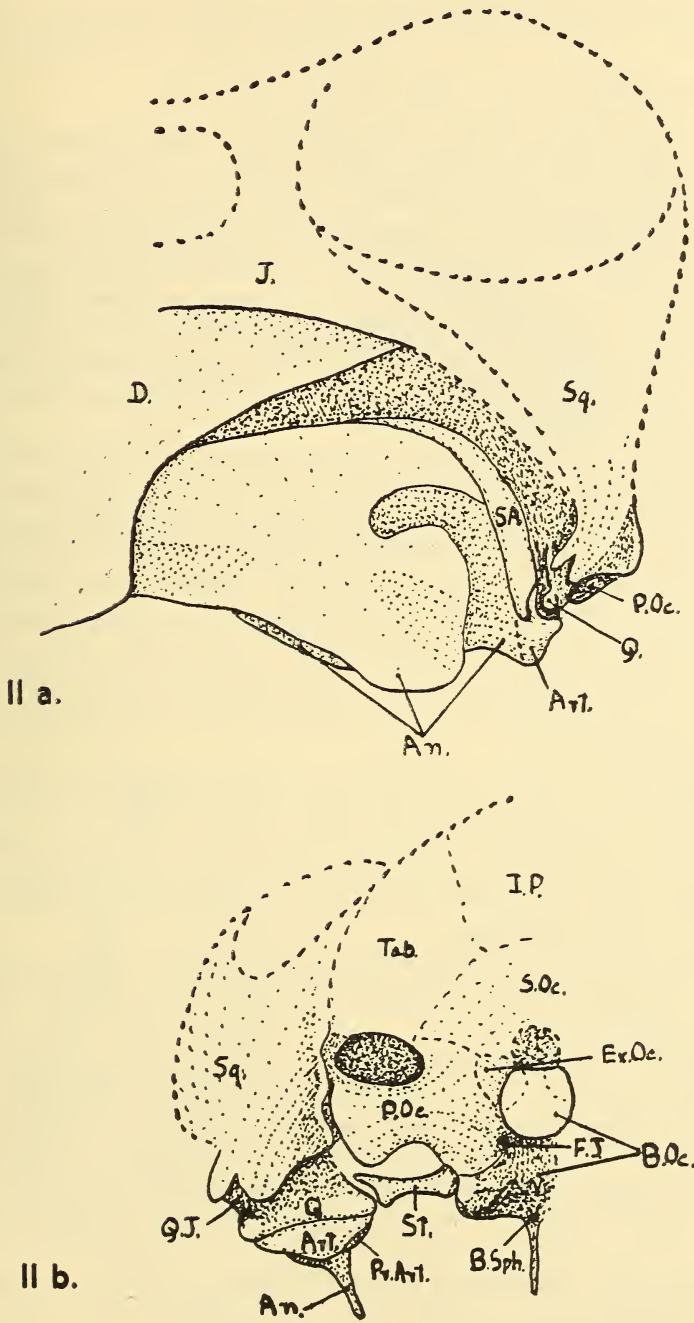


FIG. II.—*Therioides cyniscus* Gen. et Sp. Nov. S.A.M. 11888, Vindraersfontein, Beaufort West ( $\times \frac{2}{3}$ ). a, lateral view. b, occipital view.

Anterior to the descending sheet of the squamosal the paroccipital appears to abut against the median surface of the ascending pillar of the quadrate.

*THERIOIDES CYNISCUS* Gen. et Sp. Nov. (fig. II)

On the farm Vindraersfontein, Beaufort West, I collected a fair skull and fore-limb which I believe to be new and for which I propose the name *Therioides cyniscus* gen. et sp. nov. and the genotype bears the S.A.M. No. 11888. This new genus may preliminarily be described as a Pristerognathid with dental formula i. 6, c. 1, p.c. 6-7, postcanines slender and small, mentum fairly strong and squarish, quadrate situated far ventrally, maximum length about 270 mm., snout as high as broad (55 mm.), orbit well in posterior half of skull.

In *Therioides* the posterior edge of the dentary sweeps sharply in posterior direction and is directed more in the direction of the squamosal than towards the dorsally situated temporal opening.

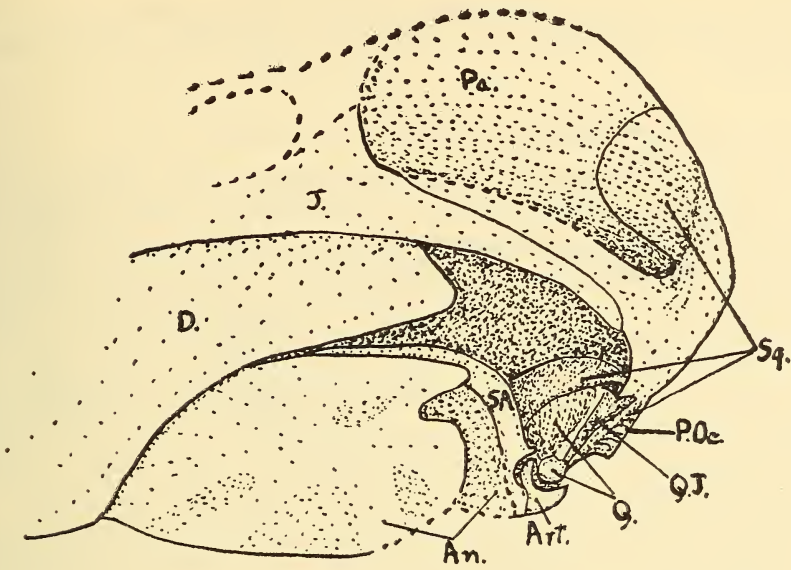
The angular has a smooth surface in its dorsal part; antero-ventrally there is a groove and another groove is directed postero-ventrally. On its lower border a thin sheet of bone lying medially projects below the edge of the outer surface. The reflected lamina is strongly developed but does not extend to the surangular. A deep notch lies dorsal to the reflected lamina and the bone surface in the notch is formed by the angular. In lateral view the surangular shows as a curved girder, anteriorly lying medially of the upper angular edge. Postero-ventrally it firmly clasps the articular. The articular is small with a slight indication of a retro-articular process. Medio-ventrally the articular is overlapped by the prearticular.

The quadrate in lateral view shows little more than the circular outline of the outer condyle above which the quadratojugal lies. In posterior view the transversely situated condylar part is partly exposed and the stout dorsal pillar-like body of the bone is seen to be overlapped by the squamosal. Medio-ventrally the rounded corner of the quadrate appears to form a surface to receive the concave distal end of the stapes.

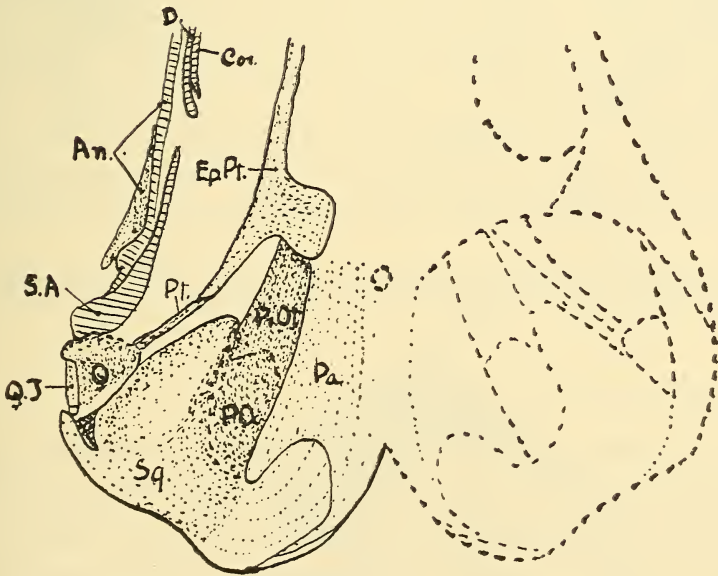
The quadratojugal is not clearly exposed but the visible bone immediately above the external rounded condyle of the quadrate is apparently the lateral part of the quadratojugal.

The postero-lateral corner of the squamosal is indented immediately above what I believe to be part of the quadratojugal. The ventral border of the posterior descending flange of the squamosal is shallowly concave and this edge probably served for the attachment of the tympanic membrane. Lateral to where the squamosal abuts against the distal end of the paroccipital, the squamosal has a high, thin sigmoid rampart forming the median wall of the auditory groove.

The ventro-distal corner of the paroccipital has a sharp edge to which the tympanic membrane was in part attached. The stapes is a slender rod in which I have not been able to detect a foramen. Its distal end has its dorsal corner prolonged and this, tipped with an extrastapedial cartilage, was probably



III a.



III b.

FIG. III.—*Pristerognathus roggeveldensis* Sp. Nov. S.A.M. 9356a, Roggekloof, Sutherland ( $\times \frac{3}{2}$ ).  
*a*, lateral view. *b*, dorsal view. A horizontal fracture makes it possible to remove the left temporal, post- and suborbital arches and show the underlying mandibular bones in horizontal section and a dorsal view of the quadrate and quadratojugal.

attached to the tympanic membrane, and the relative positions are such that the connection would be to the centre of the apparently circular tympanic membrane.

PRISTEROGNATHUS ROGGEVELDENSIS Sp. Nov. (fig. III)

Among some Pareiasaurian and Deinocephalian bones collected by Mr. A. R. E. Walker some forty years ago, I found a distorted Therocephalian skull (S.A.M. No. 9356a) representing a new species of Therocephalian, which I am provisionally including in the genus *Pristerognathus* although Seeley's genotype is of such a nature that identification with it as norm is hazardous. Specific characters of the new species, *roggeveldensis*, are: dental formula i. 6, c. 1, p.c. 5, maximum length of skull 255 mm., snout long, broader than high (52: 50 mm.); orbit in posterior half of skull; dentary with truncated posteriorly directed coronoid process. Due to the distortion the subtemporal bar is pushed up revealing much of the quadrate complex which in life would be covered. The dentary has its coronoid process truncated and directed posteriorly.

The outer surface of the angular has a number of radiating ridges separated by shallow grooves. The reflected lamina does not stretch far posteriorly and the notch is shallow. In lateral view the surangular has the same girder-like shape as in the previous forms and the articular is also very similar.

In lateral view the quadrate shows the typical circular outline of the external condyle clasped by the articular. From the condyle a thin sharp ridge stretches postero-dorsally. Anterior to this ridge and lying in a more median plane the antero-lateral face of the body of the quadrate is seen with its dorsal edge overlapped by the squamosal, which here forms a domed antero-medially directed sheet of bone. Posterior to the lateral ridge on the quadrate is some bony substance which I believe represents the small splint-like quadratojugal. In dorsal view it is seen that the quadrate lies well laterally in the skull and is situated in the angle formed by the subtemporal arch and the antero-medially directed domed sheet of the squamosal lying in the posterior part of the temporal space.

The antero-medial corner of the quadrate abuts against the slender quadrate ramus of the pterygoid and in fig. IIIb its relations to the epipterygoid can also be seen.

AN UNIDENTIFIED PRISTEROGNATHID (fig. IVa)

A shepherd on the farm Dikbome, Laingsburg District, found some weathered fragments of a Pristerognathid skeleton (S.A.M. 11959). One fragment is the remains of the right articulatory region of the lower jaw. Here the quadratojugal has been lost and the lateral aspect of the quadrate is well exposed. The condylar part of the quadrate is not fully exposed but appears to be a transversely placed roller-shaped mass posteriorly separated from the ascending pillar by a well-defined groove. The condylar mass projects laterally as a process rounded

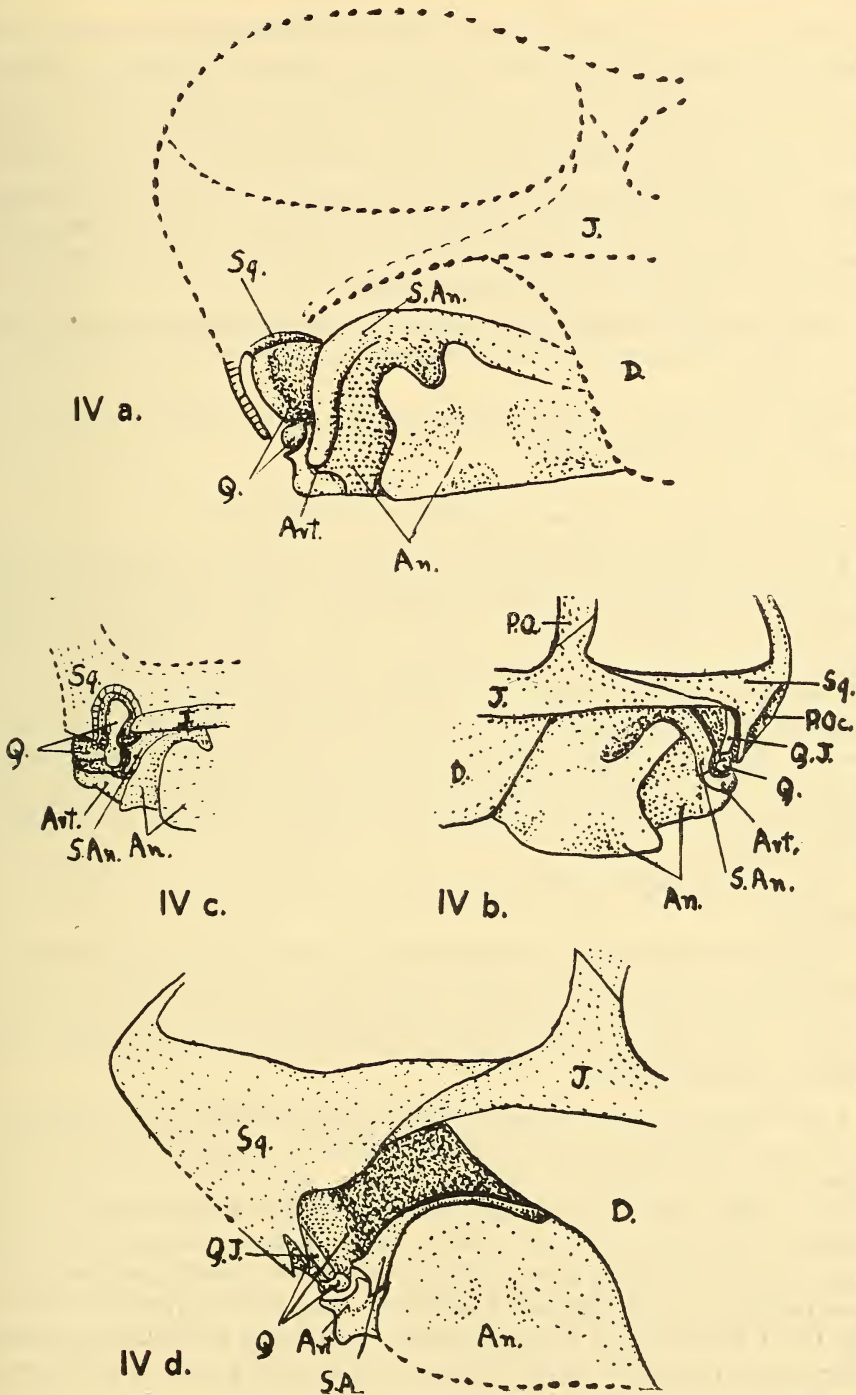


FIG. IV.—a, unidentified Pristerognathid. S.A.M. 11959, Dikbome, Laingsburg. Lateral view ( $\times \frac{3}{2}$ ). b, *Maraisaurus parvus* Gen. et Sp. Nov. S.A.M. 11944, Buffelsvlei, Beaufort West. Lateral view. Left. ( $\times \frac{3}{2}$ ). c, *Maraisaurus parvus*. Lateral view. Right. ( $\times \frac{3}{2}$ ). d, *Alopecognathus angustioriceps* Sp. Nov. S.A.M. 9342, Kröonplaas, Beaufort West. Lateral view ( $\times \frac{3}{2}$ ).



ventrally and dorsally hollowed out. It is in this dorsal hollow that the base of the quadratojugal must have rested. Above the external condyle the ascending body of the quadrate forms a rounded edge dorsally meeting the internally domed squamosal sheet. Anterior to this ridge the quadrate has a concave lateral face. The ascending process of the quadratojugal must have passed up along the posterior face of this ridge on the quadrate. On the antero-median lower corner of the quadrate a sectional face indicates where the pterygoid ramus of the quadrate emerged. The antero-dorsal face of the quadrate is covered by the domed sheet of the squamosal.

Posteriorly the descending sheet of the squamosal extended to the level of the upper edge of the condylar surface thus exposing little of the posterior face of the quadrate.

The relations of the angular, surangular and articular are in essentials as in the previously described forms.

MARSAURUS PARVUS Gen. et Sp. Nov. (fig. IV*b* and *c*)

Mr. Johannes Marais, who has for a number of years been actively interested in the fossils found on his farm, has given me a small Pristerognathid skull obtained on Buffelsvlei, Beaufort West (S.A.M. 11944). Unfortunately the snout has been broken off obliquely in front of the orbits so that the nature of the dentition remains unknown, but the rest of the skull shows it to be undoubtedly a Pristerognathid. For this form I propose the name *Maraisaurus parvus* in recognition of the work of its finder. This genus is characterized by the small size of the skull (probable maximum length 162 mm.), large orbits (34 × 26 mm.), narrow snout, squarish in cross-section; dentary not extending far posteriorly.

The posterior border of the dentary does not curve much in dorso-posterior direction.

The angulars are not very well preserved as is evident from the differences in the figures (*a* and *b*) of the two sides. It is, however, clear that the notch is situated much dorsally and that the reflected flange does not extend far posteriorly. The relations of the surangular and articular agree in essentials with the forms described above.

On the right side the lateral surfaces of the bones forming the jaw articulation have been weathered and the quadratojugal lost. As preserved the quadrate appears to be a roughly rectangular element. The condyle is a transversely situated roller with a shallow groove demarcating two nearly equal convex surfaces. Posteriorly above the condyle there is a transverse groove medially receiving the descending plate of the squamosal and laterally the base of the quadratojugal. On the left side a weathered bony edge is preserved which in fig. IV*b* I have labelled the quadratojugal believing it to flank the quadrate edge as seen in fig. IV*a* above the outwardly directed process of the external condyle.

*ALOPECOGNATHUS ANGUSTIORICEPS* Sp. Nov. (fig. IVd)

This new species is based on a well-preserved complete skull found by me on the farm Kroonplaas, Beaufort West (S.A.M. 9342). It differs from the genotype in its smaller size (252 mm.) and in having a more slender skull.

On the right side the articulatory region is fairly well exposed. An indented descending sheet of the squamosal overlaps the ascending parts of the quadrate and quadratojugal. The quadratojugal has its base resting on the upper surface of the external quadratic condyle, which is much the smaller of the two parts of the condyle. In postero-ventral view the distal corner of the paroccipital, the concave squamosal edge and the internal border of the quadratic condyle form two-thirds of a circle and it is in this space where the tympanic membrane must have been situated.

The reflected flange of the angular extends to the surangular and no angular notch is present.

With the above determinations we now know that the quadratojugal does not form part of the articulatory condyle in a number and probably in all Therocephalians. In addition to the above forms a similar condition has been found by Broom in *Lycodops* and *Hyenosaurus*, and in *Trochosaurus* my figure of the occiput (*Ann. S. Afr. Mus.*, vol. XXXI, fig. 10, p. 229) falls in line with the above interpretation.

The nature of this region in Therocephalians affords further evidence for the derivation of the Cynodonts from the Therocephalians. In addition to the cynodonts hitherto known to have the same relations of the quadrate to the quadratojugal I have a cynognathid from Winnaarsbaken (S.A.M. 11264) where the quadratojugal lies well laterally to the condyle. The well-defined auditory groove of the cynodonts is undoubtedly foreshadowed in its essential relations by the less well-defined groove seen in the Therocephalians.